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ARTICLE 1

HYPORHINA TERTIA, NEW SPECIES (REPTILIA: AMPHISBAENIA), FROM THE EARLY OLIGOCENE (CHADRONIAN) WHITE RIVER FORMATION OF WYOMING

NATURAL HISTORY SURVEY

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INTRODUCTION

Beginning with their appearance in the Paleocene (Estes, 1965), amphisbaenids are well represented in the fossil record of most of the Tertiary Period of North America. Over a half-dozen fossil genera are currently recognized, most of which are represented by well-preserved skull material. Fossil amphisbaenids exhibit no remarkable skeletal differences from extant forms and undoubtedly they all shared a common burrowing habit. Their total or partial loss of limbs, acquisition of a worm-shaped body form, compact and strongly ossified skull, and vertically depressed shovel-shaped snout are features commonly pointed to as adaptations to a subterranean habitat.

The position of the amphisbaenids within the Reptilia has been controversial and is still unsettled. A current trend is to regard them as a distinct order, Amphisbaenia, equivalent to the orders Sauria and Serpentes (Gans, 1967; Taylor, 1951). There is less agreement about classification of the amphisbaenids below the ordinal level. In a recent systematic arrangement, Vanzolini (1951) places both Recent and fossil amphisbaenids in a single family, Amphisbaenidae, which includes the four subfamilies Amphisbaeninae, Rhineurinae, Trogonophinae, and Crythosaurinae. In this grouping, Amphisbaeninae are mainly characterized as having a rounded or laterally compressed snout with laterally placed nostrils, a narrow vertical process of the premaxilla, and pleu-

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rodont dentition. Included in this group is the extant genus *Bipes* from Mexico and possibly southeastern Arizona, whose members are characterized by forelimbs. Members of the subfamily Rhineurinae are distinguished by a strong craniofacial angle, a flattened face and shovel-like snout with a sharp horizontal edge, ventrally placed nostrils, a broad, triangular vertical process of the premaxilla, and pleurodont dentition. Within this group Vanzolini places *Rhineura floridana*, restricted to Florida and representing the only other Recent genus of amphisbaenid found in North America besides *Bipes*, and all the adequately known fossil amphisbaenids of North America. Trogonophinae is distinguished most easily from the two foregoing subfamilies by an acrodont dentition. Vanzolini erected the subfamily Crythiosaurinae, to receive the presumably primitive *Crythosaurus mongoliensis* Gilmore, 1943, from the Oligocene of Inner Mongolia. It should be noted, however, that Hoffstetter (1962) has cast some doubt on the assignment of *C. mongoliensis* to the Amphisbaenia. He comments that this fossil may more correctly be interpreted, on the basis of Gilmore's figure of the type, as an ophidian. Subdivisions of the amphisbaenids by Taylor (1951) differ somewhat from those proposed by Vanzolini. Taylor recognizes among the Recent and fossil forms the families Amphisbaenidae, Bipedidae, Trogonophidae, Crythosauridae and Hyporhinidae. In this scheme Bipedidae presumably includes all the forelimbed members, and Trogonophidae those with acrodont teeth. Amphisbaenidae encompasses the remainder of the living amphisbaenids and all the previously known North American fossil forms except the Oligocene genus *Hyporhina*, which is judged worthy of family rank under the name Hyporhinidae Baur, 1893. Crythosauridae is recognized for the Mongolian genus *Crythosaurus*. Gans (1960) and Gans and Lynn (1965) have firmly documented the separation of the trogonophids as a distinct family. In a recent check list of the living amphisbaenids Gans (1967) utilizes the two family headings Trogonophidae and Amphisbaenidae (equivalent to the subfamilies Amphisbaeninae and Rhineurinae of Vanzolini), but omits subfamilial divisions. The trogonophids are generally considered the most specialized and the least primitive of the living amphisbaenids (Gans, 1960). The presence of acrodont teeth and absence of the prefrontal bone (except in *Trogonophis*) sets this group apart from the remaining living and fossil amphisbaenids, all of which have pleurodont dentition and the prefrontal bone.

When Baur (1893) erected a new family and genus of fossil amphisbaenians, Hyporhinidae and *Hyporhina*, he based his classification on a single specimen: *Hyporhina antiqua* Baur, from the late Oligocene (Whitneyan) White River Formation of Washington County, South Dakota. The specimen was a beautifully preserved skull and lower jaws.

Baur gave only a brief account, however, and it was not until 1928 that a thorough description of *H. antiqua* was given by Gilmore. A second species of this genus, *H. galbreathi*, from the Middle Oligocene (Orellan) White River Formation, Logan County, Colorado, was described by Taylor (1951). At this time Taylor reaffirmed Baur's proposal of the family Hyporhinidae, recognizing as two of the most important diagnostic features: (1) the presence of a postorbital bar formed by a postorbital bone, and (2) the near union of the premaxilla, nasals, and frontals at a single point along the dorsal midline of the skull. Vanzolini, however, assigned *Hyporhina* to the subfamily Rhineurinae.

In the summer of 1965 a field party from Carnegie Museum headed by Drs. Mary Dawson and Craig Black collected a partial skull of an amphisbaenid from the Early Oligocene (Chadronian) White River Formation near Cameron Springs, Fremont County, Wyoming. Its placement in the genus *Hyporhina* is unquestionable and it is described below as a new species.

I am indebted to Miss Helen McGinnis, of Carnegie Museum, who directed my attention to this specimen, and to my wife, Susan, who prepared the illustration.

SYSTEMATICS

Class Reptilia

Order Amphisbaenia

Family Hyporhinidae Baur, 1893

Genus *Hyporhina* Baur, 1893

***Hyporhina tertia*¹**, new species

Figure 1

HOLOTYPE: Carnegie Museum, Section of Vertebrate Fossils, CM 17179, consisting of approximately one half of the anterior part of the skull. This includes almost all the facial portion and about half of the anterior part of the palate. The right mandible is represented by most of the dentary and its dentition.

HORIZON AND LOCALITY: Early Oligocene (Chadronian), White River Formation near Cameron Springs, Fremont County, Wyoming. NW ¼ sec. 1, T. 32N., R. 90W.

DIAGNOSIS: A species more closely resembling *Hyporhina antiqua* than *H. galbreathi*. As in *H. antiqua*, there is an apparent separation of the prefrontal from the border of the orbit in *H. tertia*, though the prefrontal is not as greatly reduced as it is in *H. antiqua*. *H. tertia* differs from the two previously described species in the sutural pattern between the maxilla, frontal, and prefrontal. In *H. antiqua* and *H. galbreathi* these three bones meet in a Y-shaped sutural contact at the anteriormost point of the prefrontal, whereas in *H. tertia* an ascending process of the maxilla displaces this sutural junction to the mesial border of the prefrontal. In dorsal view, the outline of the snout of *H. tertia* is slightly less blunt, and the relative anteroposterior length of the premaxilla is greater than in either *H. antiqua* or *H. galbreathi*.

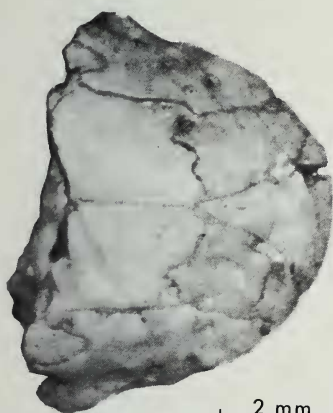
¹In recognition of this third species of *Hyporhina*, the selection of the specific name is an attempted compromise between numerical and classical taxonomy.

DESCRIPTION: The type of *Hyporhina tertia* (fig. 1) consists of a little less than half of the anterior part of the skull. The total length of the skull was probably about 10 mm. The posterior margin of the skull terminates in a somewhat ragged transverse section, which seen from above, passes from about the anterior border of the left orbit to about the middle of the right orbit. The right side of the skull is consequently more completely represented. The widest point of the skull was probably the distance between the posterior, ventrolateral wings of the maxillae. This dimension is estimated to be about 6.0 mm. in *H. tertia*. The length and width measurements of the types of *H. antiqua* and *H. galbreathi* are 10.0 mm by 5.5 mm (Gilmore, 1928), and 8.5 by 4.4 mm (Taylor, 1951), respectively.

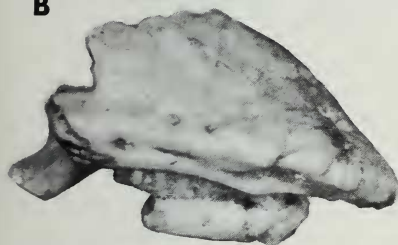
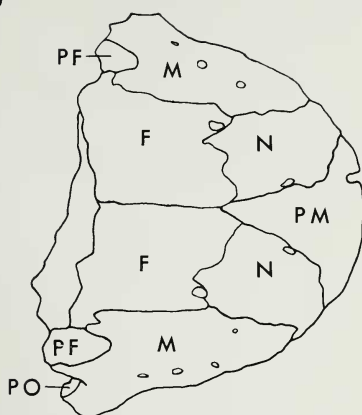
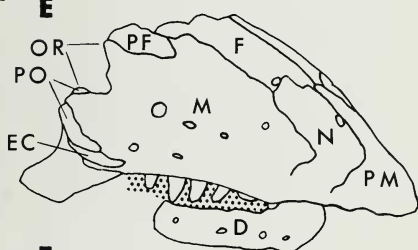
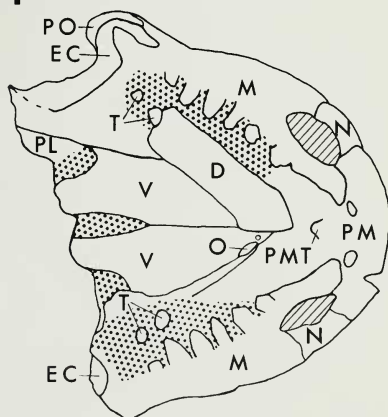
The dorsal view (fig. 1A, D) shows the premaxilla, nasals, frontals, maxillae, prefrontals, and a small portion of the postorbital. The premaxilla is triangular in outline with the width exceeding the length only slightly. Posteriorly it barely wedges between the frontals, narrowly excluding the nasals from medial contact. In the type specimens of *H. antiqua* and *H. galbreathi* the premaxilla is separated from the frontals medially by a narrow contact of the nasals. In a specimen referred to *H. galbreathi* by Taylor (1951), however, a premaxilla-frontal contact is noted. This feature may be variable in this group.

In ventral aspect (fig. 1C, F), the premaxilla has a slightly raised edge that is continuous with the anterior margin of this bone. Just posterior to this ridge, in a broadly concave depression, are two well-marked foramina located near the midline. Immediately posterior to its small contribution to the anteromedial border of the external naris, the premaxilla is sharply waisted by an anterior process from each maxilla, which forms the inner border of the naris. On a line connecting the mid-medial margins of the external nares, the premaxilla makes a sharp step dorsally as it enters the oral cavity. Medially and on the vertical aspect of this step, there is a single, poorly developed tooth that points backward. Both *H. antiqua* and *H. galbreathi* possess a similar, single premaxillary tooth. Behind this and within the oral cavity, the premaxilla sends out two long, widely diverging processes that extend back to about the third maxillary tooth and at a level dorsal to the bases of the maxillary teeth.

Fig. 1. *Hyporhina tertia*, new species. A, dorsal, B, lateral, and C, ventral views of type, CM 17179. D., E., and F. are outline sketches of A., B., and C. Size indicated by 2-mm scale. Stippled areas represent matrix. External nares indicated by oblique ruling. Abbreviations: D, dentary; EC, ectopterygoid; F, frontal; M, maxilla; N, nasal; O, orifice of Jacobson's organ; OR, preserved limits of orbital rim; PL, palatine; PF, prefrontal; PM, premaxilla; PMT, premaxillary tooth; PO, postorbital; T, tips of dentary teeth embedded in matrix; V, vomer.

A

2 mm

B**C****D****E****F**

Dorsally, the premaxilla is flanked by the nasals, except for the tip of the posterior process, which is wedged between the frontals. The nasals narrow and diverge toward the anterior, then widen somewhat before turning back under the rim of the snout to form the anterolateral border of the external nares. There is a well-defined foramen on the border of the nasal, midway along the length of the dorsal, naso-premaxillary suture.

The large frontals are undoubtedly incomplete. Their posterior margins (figs. 1A,D) end in a ragged, broken edge and as much as a third of the frontals may be missing. The remaining portions of the frontals are subrectangular in outline, except at their posterolateral corners, which swing laterally to contact the small prefrontals. In the anterolateral corner of each frontal is a large foramen.

The maxilla is the most extensive element preserved in *H. tertia*. It forms the anterior part of the orbit (figs. 1A,B,D,E), then swings dorsally and posteriorly in the form of a narrow process to contribute to the dorsal border of the orbit. The exact dorsal extent of this process is impossible to determine, and it is very likely that, posterior to the prefrontal, a descending, lateral process of the frontal also contributed to the dorsal margin of the orbit where it made contact with the maxillary process. This would be similar to the condition in *H. antiqua*. A short, posteromedially directed process of the maxilla excludes the anterior third of the medial border of the prefrontal from contact with the frontal. This process is absent in both *H. antiqua* and *H. galbreathi*, where the entire medial border of the prefrontal articulates with the frontal. A row of three to four well-marked foramina runs roughly anteroposteriorly across the mid-lateral surface of the maxilla. Ventral to this series of foramina the external surface of the maxilla makes a sharp ventromedial turn toward the maxillary dentition, forming a smoothly rounded ridge that underhangs the lateral bases of the teeth (figs. 1C,F). Parallel and lateral to this ridge is a broadly concave channel, perforated by a pair of relatively large dental foramina. Medial to the maxillary dentition, there is a wide palatine shelf of the maxilla, notched anteriorly to receive the posterior process of the premaxilla. Posteriorly, the shelf meets the ectopterygoid (preserved most completely on the right side of the palate) in a smooth curve.

The maxilla supports a row of six simple, conical teeth. They are pleurodont or subpleurodont in attachment and inclined posteromedially. The second is larger than the first and third. The third through fifth increase in size to about that of the second, and the sixth and last tooth is much reduced over the fifth. Six pleurodont maxillary teeth are reported in *Hyporhina galbreathi* (Taylor, 1951), whereas in *H. antiqua*, Gilmore (1928:49) reports that the maxilla "carries four small, pointed teeth. . . . that appear to be acrodont in attachment."

The right prefrontal (figs. 1A,B,D,E) is best represented in the type of *H. tertia*, and, although a small portion of this element may be missing posteriorly, it differs noticeably from the prefrontals in the types of *H. antiqua* and *H. galbreathi*. The prefrontal in *H. galbreathi* is unique in being large and forming more than a third of the border of the orbit (Taylor, 1951), rather than being completely separated from the orbit by a process of the maxilla, as in *H. antiqua* and *H. tertia*. In *H. tertia*, the prefrontal is relatively large and is positioned almost directly dorsal to orbit, whereas in *H. antiqua* it is about one third as large, and is located anterior to the orbit.

The postorbital bone (figs. 1B,E) is partially preserved on the right side of the skull. It is seen as a narrow splint of bone, wedged ventrally between the maxilla and a slender external process of the ectopterygoid. The postorbital can be seen ventrally on the lower border of the orbit, where it sends forward a projection that contributes substantially to the ventral border of the orbit. Above this point the postorbital has been broken away. If complete, the postorbital undoubtedly would have continued dorsally as a slender bar enclosing the orbit behind, and uniting with the frontal and parietal above, as reported in *H. antiqua* and *H. galbreathi*. In neither of these forms, however, is there any indication that the postorbital forms any part of the ventral rim of the orbit.

The paired vomers (figs. 1C,F) meet in a straight median suture and occupy a broad triangular space between the palatine shelves formed by the maxillaries and the posterior processes of the premaxilla. The anterior tip of the vomer abuts against the premaxilla for a very short distance laterally, while posteriorly its lateral border appears to insert dorsal to the palatine shelf of the maxilla. At about the level of the posterior maxillary tooth the vomers become constricted and slightly separated as they extend caudally in two narrow tongues. Their posterior extent is not preserved. The incompletely preserved, trough-shaped palatines occupy the area lateral to the posterior processes of the vomers. The narrow depressed area between these processes (now filled with matrix) probably received the parasphenoid. A very faint foramen pierces the vomer near its anterior limit. Immediately posterior to the vomer-premaxillary contact, the lateral margin of the vomer has an oblong notch, closed laterally by the anterior tip of the palatine shelf of the maxilla. This is presumed to be the opening for Jacobson's organ.

The right ectopterygoid is nearly complete. Seen from below, it appears as a band of bone that smoothly arches anteromedially to meet the maxilla. A small, finger-like extension of the maxilla inserts ventrally on the ectopterygoid, giving it an S-shaped pattern. On the external surface of the skull (figs. 1B,E), the ectopterygoid appears as a

splint of bone wedged between the ventral border of the postorbital and the maxilla. In comparison, the ectopterygoid in *H. galbreathi* is greatly reduced and does not swing laterally to reach the external surface of the skull (Taylor, 1951). In *H. antiqua* the palatal region is obscured by the closely attached mandibles (Gilmore, 1928). Judging from Gilmore's figures, however, it would appear that the ectopterygoid is not exposed on the external surface of the skull.

The lower jaws are represented by the dentaries only. Little of the left dentary remains, as part was broken away in preparation. The tips of some of the teeth (figs. 1C,F) remain embedded in the matrix left on the palate. The right dentary is about three-fourths complete and is closely applied to the skull. Anteriorly it is complete, and there is a moderately well developed symphysis. The dentary remains relatively uniform in width and depth throughout its length, and when complete held seven teeth. A row of small foramina runs the length of its labial surface. The first five dentary teeth are still intact, though partially hidden by matrix. They are simple conical pegs attached in pleurodont or subpleurodont fashion. All that remains of the last two teeth are the tips of their crowns embedded in matrix on the maxilla. These two teeth would have attached to the missing posterior portion of the dentary. The first and fourth maxillary teeth are nearly equal in size and are much larger than the others. The second and third increase in size posteriorly. The fifth through seventh decrease posteriorly. The lower jaw is not known in *H. galbreathi*, and in *H. antiqua* the number of dentary teeth could not be determined by Gilmore (1928).

DISCUSSION

In 1893, Baur described a new genus and species of fossil amphisbaenid, *Hyporhina antiqua*, from the Late Oligocene (Whitneyan) White River Formation of South Dakota, and proposed the new family Hyporhinidae for its reception. In 1951, Taylor described a second species of this genus, *H. galbreathi*, from the Middle Oligocene (Orellan) White River Formation of Colorado. He agreed with Baur that *Hyporhina* is worthy of family rank. In this report a third species of *Hyporhina* is described, *H. tertia*, from the Early Oligocene (Chadronian) White River Formation of Wyoming. All three species are very similar in general form and are clearly related at the generic level.

The character considered most important by Baur (1893) and Taylor (1951) for the establishment of the family Hyporhinidae was the presence of a postorbital bone. Undescribed fossil amphisbaenids in my possession from the Eocene Bridger Formation of Wyoming and from the Oligocene and Miocene John Day Formation of Oregon have a postorbital bone that closes the orbit from behind in the same manner as in *Hyporhina*. On the family level, these specimens are clearly dis-

tinct from *Hyporhina*, and their possession of a postorbital is not a good criterion for establishment of the family Hyporhinidae. Further, there is the likelihood that some of the previously described fossil amphisbaenids may have had a postorbital bone. The postorbital bone is a rather delicate element and there is a tendency for it to be missing in forms known to have it. It is highly probable, therefore, that both postorbitals could be lost through imperfect preservation in a fossil amphisbaenid that has been used as the basis of a new taxon diagnosed as never having this bone.

Although the presence or absence of a postorbital may have little or no taxonomic value, members of the genus *Hyporhina* have a suite of characters that are distinctive enough to warrant separate family ranking. A hyporhinid feature seemingly unique among fossil amphisbaenids is the extremely long, posteriorly directed, paired palatal processes of the premaxilla. In *Hyporhina* these processes share greatly with the maxillae in the formation of a palatine shelf. In other fossil amphisbaenids where this region has been described, the premaxilla is excluded by the maxilla from making any sizeable contribution to the palatine shelf.

The near meeting of premaxilla, nasals, and frontals at a common point on the dorsal surface of the skull is also a character that sets *Hyporhina* apart from all previously described fossil forms. Unique and probably related to this feature is the extreme shortness and bluntness of the facial portion of these shovel-snouted forms.

The three recognized species of *Hyporhina* can be arranged in a morphological series that exhibits a tendency toward a pronounced reduction of the prefrontal bone. The Middle Oligocene *H. galbreathi* would represent the primitive condition, in which the prefrontal is of normal amphisbaenid proportions and forms more than one third of the dorsal border of the orbit. The Early Oligocene *H. tertia* would represent the next stage in this series. Here the prefrontal is slightly reduced and has become separated from the orbit by a dorsal process of the maxilla. And finally, in the Late Oligocene *H. antiqua*, the prefrontal has become reduced to a very small, triangular bone that is located anterior to the orbit and is excluded from the border of the orbit by a process from the frontal above and the maxilla below. This morphological series, though not following exact chronological sequence, suggests that the hyporhinids were well along by Late Oligocene times in what would appear to be an elimination of the prefrontal. Among the present day amphisbaenids, only in the advanced and primarily African trogonophids has there been a loss of the prefrontal.

The unique features of *Hyporhina* listed above are not seen in any other known group of fossil amphisbaenids. This, coupled with a geologic history that spans at least the Oligocene, argues in favor, though

on somewhat different morphological grounds than that offered by past workers (Baur, 1893; Taylor, 1951; Vanzolini, 1951), of recognizing this group as part of a distinct lineage deserving of family status. Among the extant forms, I am aware of only one genus, *Monopeltis* (Africa), that closely approaches *Hyporhina* in cranial morphology. In a description of *Monopeltis c. capensis* given by Zangerl (1944), all the key characters noted above for *Hyporhina*, excluding the variable prefrontal bone, are duplicated to some degree. The occurrence of these two groups on widely separated continents is the only major obstacle to suggesting a possible direct relationship. There is neither evidence that the Hyporhinidae survived later than the Oligocene, nor is there any known form that can be seriously considered ancestral to the Hyporhinidae.

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